Macro- and microstructure of shell and operculum in two Recent gastropod species, *Nerita* (*Theliostyla*) *albicilla* and *Cinnalepeta pulchella* (Neritopsina: Neritoidea)

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Abstract. The shell and opercular structures of *Nerita* (*Theliostyla*) *albicilla* and *Cinnalepeta pulchella* were described and compared with those of other extant members of Neritopsina. The shell of *N.* (*T.*) *albicilla* is composed of four layers: the outermost prismatic layer, followed by the simple crossed-lamellar layer, the myostracum, and the inner complex crossed-lamellar layers. The operculum consists of three prismatic layers deposited on both sides of an organic layer. *C. pulchella* also has a four-layered shell, but lacks an operculum. The outer layer is a homologous structure. The shells of Recent neritopsine families can be categorized into a four-layered group (Neritiliidae, Neritidae, and Phenacolepadidae) and a three-layered group (other families). In contrast, opercular structure is markedly variable in the Neritopsina, and little correlation can be established in the light of phylogenetic evolution or adaptation.

Introduction

Neritopsina is a phylogenetically distinct gastropod clade which originated in the Ordovician (Bandel and Frýda, 1999). The Recent members share characteristic apomorphies of odontophoral cartilages and muscles, anterior digestive tract, reproductive organs, and nervous system (Haszprunar, 1988; Ponder and Lindberg, 1997; Sasaki, 1998) and exhibit successful adaptive radiation in a wide range of habitats in deep-sea hydrothermal vent or hydrocarbon seep, submarine cave, intertidal rocky shore, and nonmarine aquatic and terrestrial environments (Ponder, 1998; Sasaki, 1988). It is also particularly interesting that neritopsines have rich fossil records since the early Paleozoic (Bandel, 1992; Bandel and Frýda, 1999), and that ancient taxa like *Neritopsis* have survived as relics in cryptic habitats (Kase and Hayami, 1992).

Among hard-part characters, shell structure, along with larval shell morphology, is of primarily taxonomic importance for studies uniting fossil and Recent taxa of Gastropoda (Bandel, 1982; 1988; 1991; Bandel and Geldmacher, 1996). In Gastropoda, Patellogastropoda are known to exhibit remarkable diversification of the shell microstructure (MacClintock, 1967; Lindberg, 1988, 1998). Grouping by

shell structure corresponds well to the anatomical division of supraspecific taxa, and therefore enables paleontologists to allocate fossilized taxa within an anatomy-based systematic scheme (Kase, 1994; Kase and Shigeta, 1996; Lindberg and Hedegaard, 1996; Hedegaard *et al.*, 1997). As for other gastropod higher taxa, Vetigastropoda are typically characterized by the apomorphic occurrence of columnar nacreous structure, although some taxa have supposedly lost it secondarily (Hedegaard, 1997). In the Apogastropoda, which is a huge clade including Caenogastropoda and Heterobranchia, the shells are composed primarily of several layers of crossed-lamellar structure and differences between distantly related subclades within it are in general minor (Bøggild, 1930; Bandel, 1979; Togo and Suzuki, 1988). At relatively lower rank, however, some striking differences can be revealed by detailed comparison, as was shown in littorinid genera by Taylor and Reid (1990).

Despite its unique phylogenetic status among gastropods, little discussion has been devoted to exoskeletal evolution of Neritopsina as compared to other major taxa of molluscs. The current knowledge of neritopsine hard-part structures is derived from only a limited amount of literature, and in addition, most data have been documented in simple format with a few or no illustrations. To increase data quality and

quantity on neritopsine hard parts, this study aims to describe the shell and opercular structures of two Recent species in detail from the macro- to microscopic level. The results of the observations were compared with the published data of other neritopsines in the literature, and their similarities and dissimilarities were discussed from phylogenetic and adaptational viewpoints.

Material and methods

The shells of *Nerita* (*Theliostyla*) *albicilla* were collected alive from an intertidal zone at Banda, Tateyama, Chiba Prefecture, central Japan, and living specimens of *Cinnalepeta pulchella* from Tosashimizu, Kochi Prefecture, southwest Japan were provided by Dr. Shigeo Hori. In the laboratory, the macroscopic morphology and the distribution of shell layers based on texture were first observed under a binocular microscope. Then, the shell was crushed with a hammer, and the original position of fragments was labeled before cleansing in bleach for 12 hours and later in running water for 30 minutes. The fresh fracture of shell fragments was observed with a scanning electron microscope (SEM).

The description of microstructure was made on layer distribution, boundary between layers, form of crystal aggregation, and orientation and morphology of first- to third-order units (major to minor structural arrangement). The descriptive terminology of microstructure follows Carter and Clark (1985) and Kano and Kase (2000b). The two terms, "crossed lamellar" and "complex crossed lamellar," are abbreviated as "CL" and "CCL."

Terms for orientation were based on the following criteria: (1) "anterior-posterior" direction was determined by body axis of the animal, and (2) "adaxial-abaxial" distinction relative to coiling axis of whorls was used to indicate relative position along inner-outer lips of the aperture.

The samples used in this study are preserved in the University Museum, the University of Tokyo (UMUT).

Description

Order Neritopsina Cox and Knight, 1960
Superfamily Neritoidea Rafinesque, 1815
Family Neritidae Rafinesque, 1815
***Nerita* (*Theliostyla*) *albicilla* Linnaeus, 1758**

Figures 1–5

Shell.—The shell is elongate along the anterior-posterior axis of the animal. The spire is completely depressed as a part of rounded whorls, and the external part of the shell is mostly occupied by a large body whorl and an extended aperture.

The outer lip of the aperture is thickened and indented with elongate denticles, being arranged parallel to the apertural margin. The inner lip spreads widely over the body whorl to form a robust inductura.

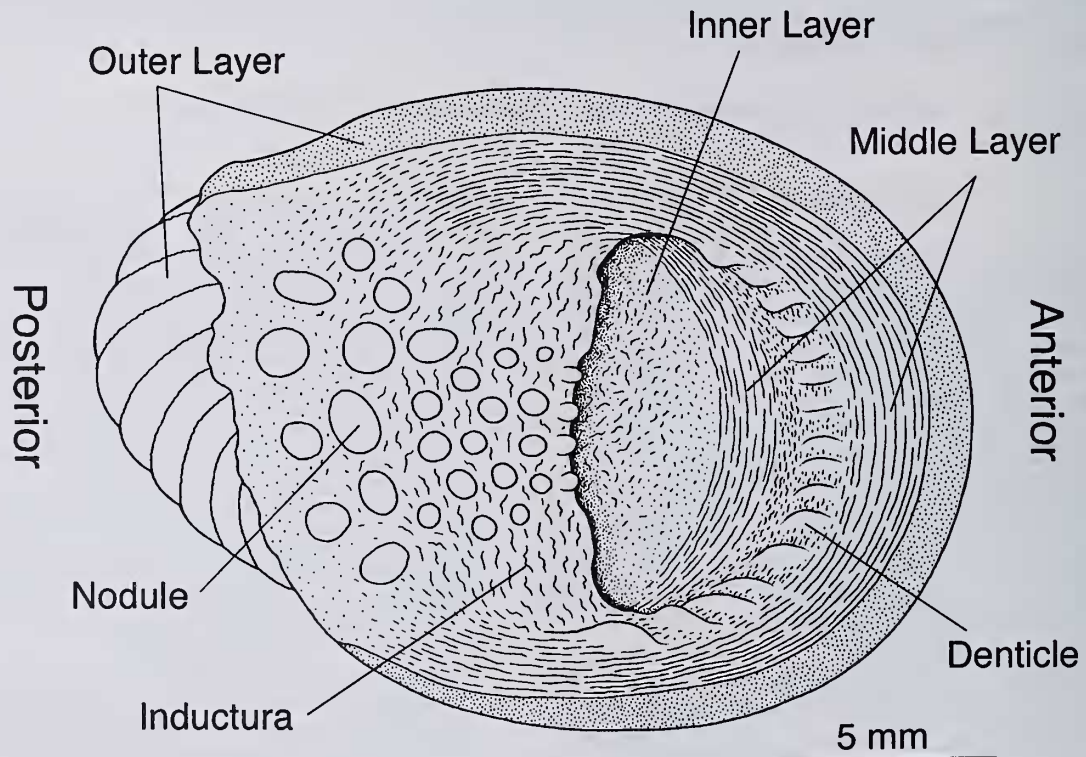The shell wall near the outer lip consists of three layers;

Figure 1. Apertural view of the shell of *Nerita* (*Theliostyla*) *albicilla*. The sculpture and texture of the surface are depicted slightly schematically. The dark outer layer is distinguished by fine-grained smooth surface, the middle layer exhibits dense linear pattern of CL structure, and most of the inner layer is visible as irregularly oriented lines.

i.e. outer and middle layers and a distinct denticular zone (Figure 1). The outer layer contains black pigments, encircles the apertural margin, and makes a clear contrast with the pale inner layer. Microstructurally this layer is formed of a thick aggregate of short prisms (Figure 3A), which can be identified as blocky prismatic structure. The prisms attain less than 4 µm in length and 1 µm in width. The middle layer is composed of comarginal simple CL structure (Figure 3B–E). The linear lines of the first-order units are clearly visible on the inside of the aperture even at low magnification (Figures 1, 2). The denticular zone is built up of a thin layer of irregularly crossed fine crystals (CCL structure). The denticles do not continue spirally toward the inside of the aperture but remain in the identical position due to resorption.

The inner lip margin is shallowly curved with two to four small nodules (Figure 1). The surface of the inductura is roughened with nodules of various size, and their number and distribution are considerably variable intraspecifically. The inductura, especially near the inner lip, shows an irregular texture reflecting the first-order arrangement (Figure 1). There is no sharp boundary between the CL structure of the middle layer and the CCL structure of the inductura. The linear patterns of the middle layer gradually merge into the irregular patterns of the inductura (Figure 1).

Shell muscle scars are separated into a disjunct pair corresponding to right and left shell muscles (see Sasaki, 1998:

fig. 73a). The left scar is located on the basal side near the inner lip (Figure 2), while the right one lies on the opposite, apical side. The scars are deeply impressed on the interior shell surface and reflect the form of muscles which are divided into bundles (Figure 2). The myostracum from the left scar is formed as a vertical stack of irregular prisms (Figure 3F), and its thickness exceeds 80 µm in an adult shell. The myostracum from the right scar is immediately resorbed and not traceable in most sections.

The inside of the visceral part of the shell is extensively resorbed and reorganized as a hollow space without a true columella. A platy septum connecting the inner lip and apical wall of the shell is secreted and inserted into the narrow space between head-foot and uncoiled visceral mass of the animal (Figure 2; see also Sasaki, 1998: fig. 73a). The septum, inner lip, inductura, and the interior of whorls are all constructed as a continuity of the inner layer (Figure 2). The layer has CCL structure: lathy third-order units are set radially to form fan-shaped second-order units, which in turn are vertically stacked to form wedgelike first-order units which are irregularly oriented and interdigitate with one another (Figure 3G, H). The structure appears as spinous crossing prisms at the initial stage of formation near its growth front. Several very thin prismatic sublayers are inserted in a thick CCL layer of the inductura (Figure 2).

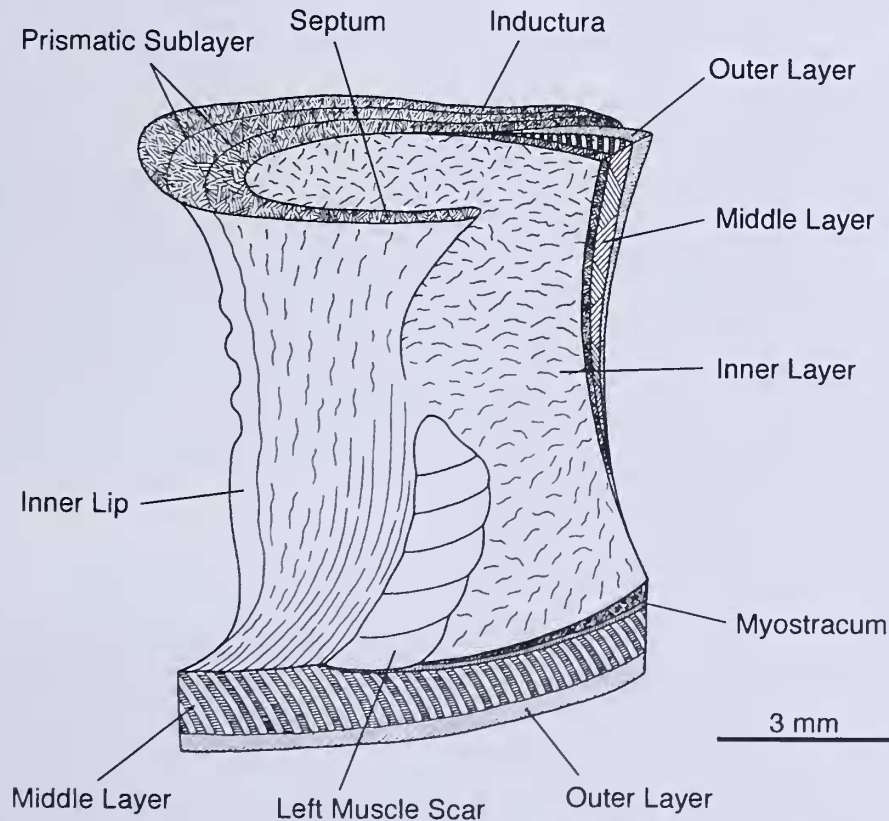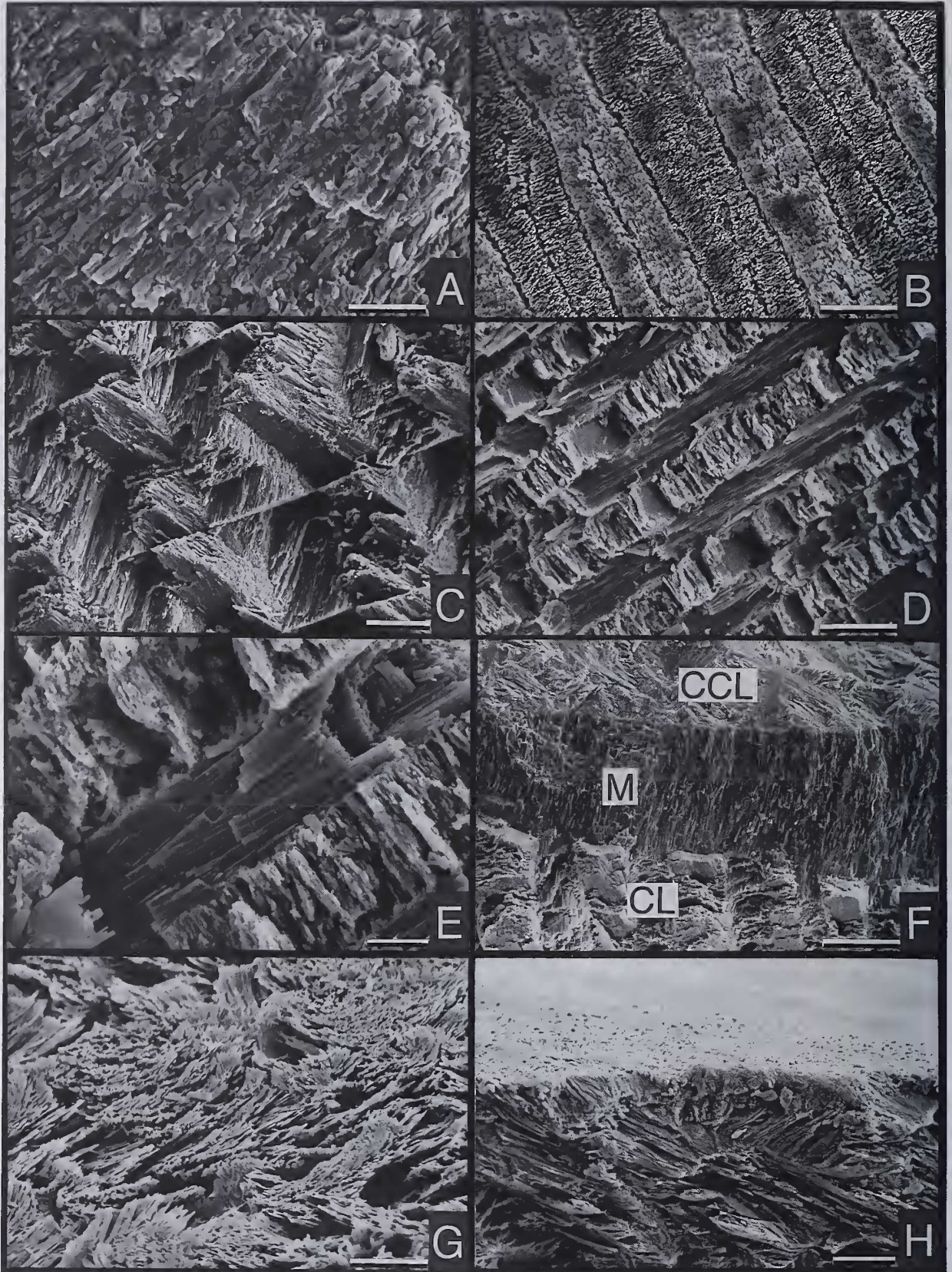*Operculum.*—The operculum is heavily calcified with a distinct apophysis (Figure 4A, B). The exterior surface is

Figure 2. Schematic representation of inner part of whorls of *Nerita* (*Theliostyla*) *albicilla*, seen from the outer lip of the aperture. Shell layers on cut planes are illustrated based on the results of observations with SEM.
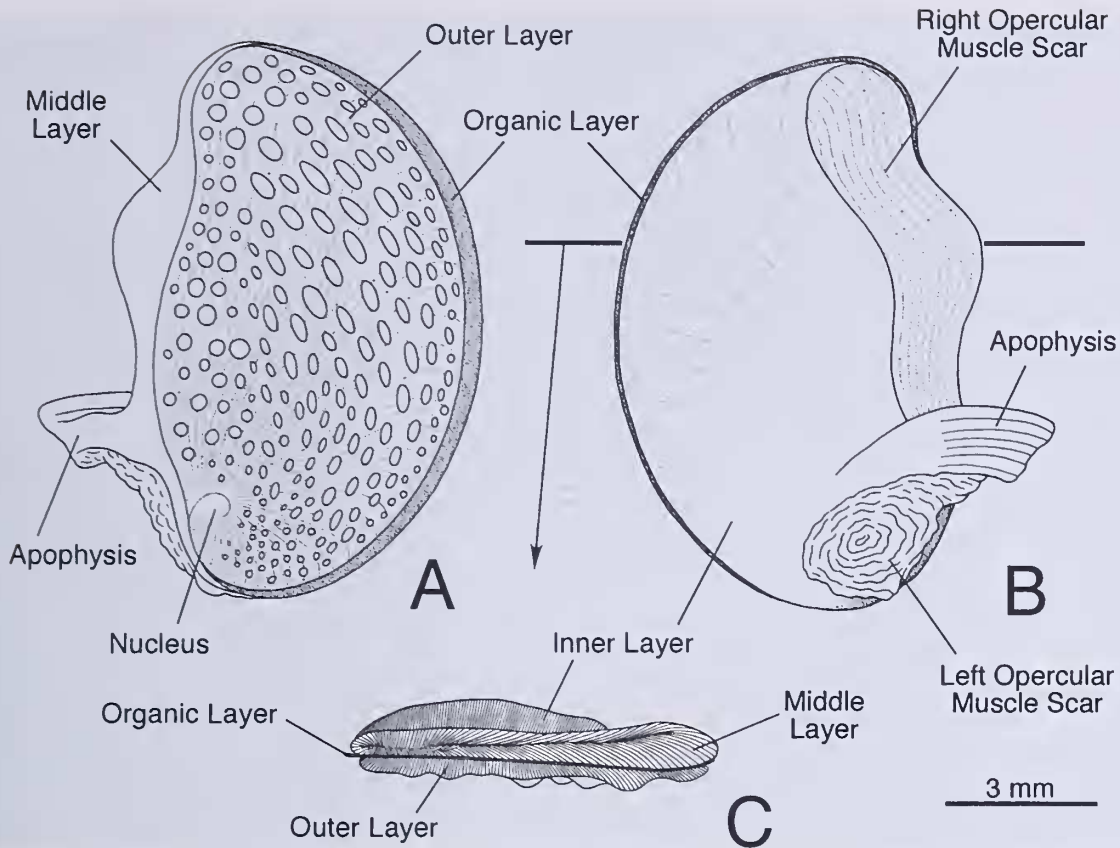
Figure 4. Operculum of *Nerita* (*Theliostyla*) *albicilla*. **A.** Exterior view. **B.** Interior view. **C.** Vertical section showing the growth direction of prisms in three calcified layers. Cut position is shown in Figure B with solid lines.

covered with small nodules which tend to be arranged spirally (Figure 4A). The nucleus lies on the adaxial basal side at the origin of the spiral growth line.

The calcified part of the operculum can be divided into three layers (Figure 4C). The outer and inner layers are both composed of slightly inclined, nearly vertically ordered prisms (Figure 5B, D). In the middle layer, prismatic crystals are arranged in a spherulitic form (Figure 5C). A very thin organic layer, the homologue of the noncalcified operculum of other gastropods, is mostly concealed between the outer and middle layers and appears only along the abaxial margin (Figure 4A, B).

The adaxial side of the operculum is partially embedded in the pedal musculature of the animal and marks clear depressions of muscle scars (Figure 4B). The left scar is small and very irregular with nearly concentric lines (Figure 5A). The right scar is elongated along the abaxial margin and smoothened.

Family Phenacolepadidae Rafinesque, 1815
Cinnalepeta pulchella (Lischke, 1871)

Figures 6, 7

Shell.—The shell is completely limpet-shaped and elongated along the anterior-posterior axis (Figure 6). The apex is situated at the posterior end of the shell. The larval shell in the original position of the apex is involved between whorls and inner lip during growth and no longer visible in a fully matured adult shell. The inside of the apex is slightly remoulded by resorption, but a septumlike structure is not constructed in this species.

The shell consists of four layers, including the myostracum. The outer layer is composed of fine homogeneous crystals (homogeneous structure) (Figure 7A, B). The middle layer is of commarginal simple CL structure. It is somewhat transparent, and clearly demarcated from the

← **Figure 3.** SEM micrographs of shell microstructure of *Nerita* (*Theliostyla*) *albicilla* (UMUT RM27950). **A.** Blocky prismatic structure of outer layer. Scale = 5 μm. **B.** Outcrop pattern of simple CL structure near outer lip of aperture. Scale = 20 μm. **C.** Oblique view of the fracture of simple CL structure in the middle layer. Scale = 20 μm. **D.** Horizontal view of the fracture of the same layer. Scale = 20 μm. **E.** Enlarged view of the same layer, showing the arrangement of the third-order units of CL structure. Scale = 5 μm. **F.** Vertical fracture of the myostracum inserted between inner (above) and middle (below) layers. M = myostracum. Scale = 40 μm. **G.** Outcrop pattern of CCL structure on interior surface of the whorls. Scale = 20 μm. **H.** Vertical fracture of the same structure in inner layer. Scale = 20 μm.
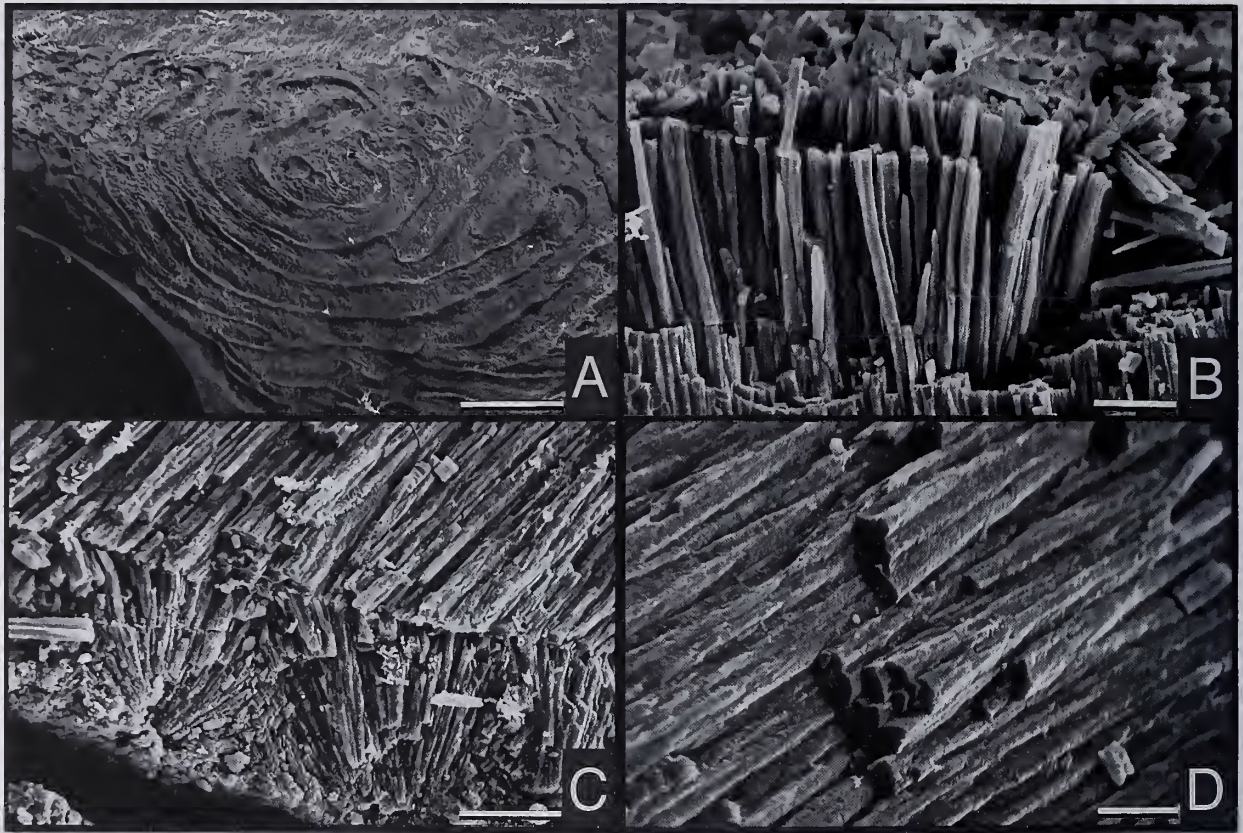
Figure 5. SEM micrographs of opercular microstructure of *Nerita* (*Theliostyla*) *albicilla* (UMUT RM27951). **A.** Surface of left opercular muscle scar with irregularly concentric lines. Scale = 250 µm. **B.** Vertical fracture of outer prismatic layer. Scale = 10 µm. **C.** Vertical fracture of the middle layer, showing spherulitic arrangement of prisms. Scale = 10 µm. **D.** Oblique view of a section of inner prismatic layer. Scale = 5 µm.

brown outer layer. Linear patterns of the first-order units of the middle layer are parallel near the shell margin and increase in irregularity toward the center (Figure 6). In the typical regular simple CL structure near the apertural margin, the crossing angle of the second-order lamellae is approximately 125 degrees. The inner layer consists of a CCL structure with fan-shaped second-order and lath-type third-order units (Figure 7D, E).

The inner lip projects inside along the posterior apertural margin and is formed as an extension of the CL structure of the middle layer (Figure 6). It lies between the ventral posterior of the visceral mass and the dorsal posterior of the foot of the animal.

The muscles scars are distributed in an elliptical form, keeping an almost constant distance from shell margin (Figure 6). They are inserted by two kinds of muscles of the animal: the thicker horseshoe-shaped part is the attachment of pedal retractor muscles (including head retractors in part), and the thinner anterior part is that of pallial muscle hanging the mantle onto the interior of the shell. The myostracum from these muscle scars is a thin layer of vertically oriented columnar prisms (Figure 7C). The surface of the pedal muscle scar is deeply impressed and exhibits a ridgelike

rough sculpture (Figure 7F).

Operculum. — The operculum is completely absent and was not found in any section of pedal musculature as already described by Sasaki (1998: 120).

Discussion

Recent forms of neritopsine gastropods comprise nearly 120 genera and subgenera (Vought, 1989). Although different opinions exist regarding suprageneric systematics, the Recent forms can be grouped into at least seven families, namely Neritopsidae, Hydrocenidae, Helicinidae [this family may be divided into Ceresidae, Proserpinidae, and Helicinidae (Thompson, 1980)], Titiscaniidae, Neritiliidae, Neritidae, and Phenacolepadidae ["Shinkailepadidae" is probably included here] (Ponder, 1998; Sasaki, 1998; Bandel and Frýda, 1999; Kano and Kase, 2000a, b; see also Sasaki, 1998 for their anatomical basis). Information on their shell and opercular structure can be summarized as follows.

Shell structure of Recent Neritopsina

Shells of only ten genera belonging to six families have

Anterior

Outer Layer

Pallial Muscle Scar

Middle Layer

Pedal
Muscle
Scar

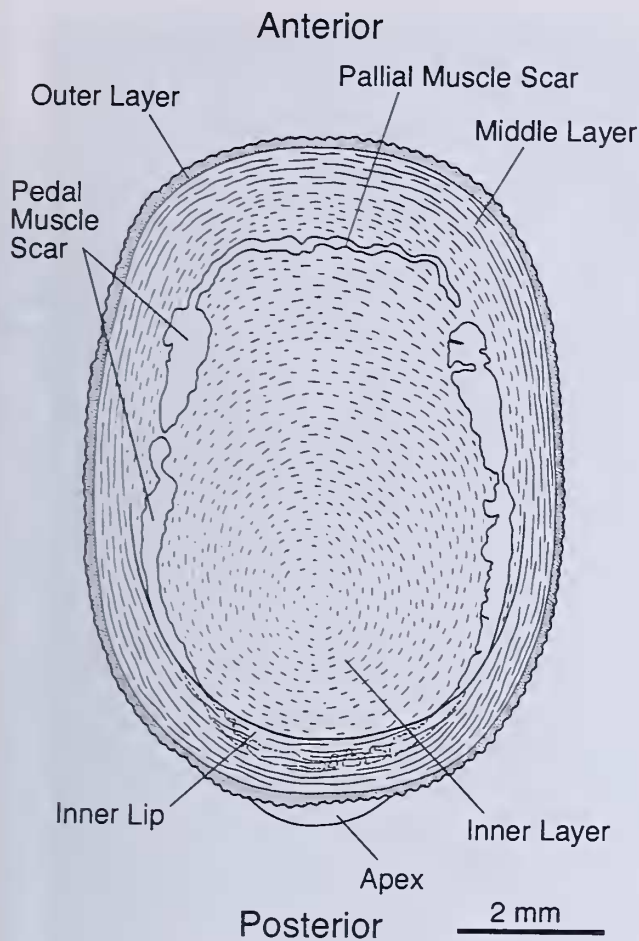Inner Lip

Inner Layer

Apex

Posterior   2 mm

Figure 6. Apertural view of *Cinnalepeta pulchella*. The sculpture texture of the surface is illustrated slightly schematically. The outer layer is separated from other parts by deep brown color, the middle layer is represented by concentric lines of CL structure, and the inner layer is visible as fine irregular lines of CCL structure.

been investigated at the microstructural level (Table 1). Major differences among suprageneric taxa are found mainly in the number of shell layers, the microstructure of each layer, and the crystal forms of carbonate calcium (aragonite-calcite).

(1) Neritopsidae: This family is characterized by intact inner upper whorls in contrast to other families with resorbed, hollow whorls inside (Bandel and Frýda, 1999). The shell wall of *Neritopsis radula* was described as "having two crossed-lamellar layers" by Batten (1979), but according to Suzuki *et al.* (1991), it is composed of an aragonitic outer layer of CL structure and an aragonitic inner layer of "proto-crossed lamellar, irregular prismatic, homogeneous, and complex crossed lamellar structures." The mixture of four microstructures in the inner layer of *N. radula* is, therefore, a unique feature among Neritopsina.

(2) Hydrocenidae: The shell of *Georissa japonica* has three layers including the myostracum: the thicker aragonitic outer layer is of CL structure, and the thinner inner aragonitic

layer is primarily of irregular prismatic structure and subsidiarily of "protocrossed-lamellar" structure (Suzuki *et al.*, 1991).

(3) Helicinidae: The shell of *Waldemaria japonica* (Helicininae) has almost the same structural design as that of *Georissa japonica*, but the inner layer is mainly occupied by "protocrossed-lamellar" structure (Suzuki *et al.*, 1991). Microstructural data have not been provided for any other member of these families.

(4) Titiscanidae: This family totally lacks the shell at least at the adult stage (Bergh, 1890; Taki, 1955).

(5) Neritiliidae: This group had been extremely poorly known taxonomically but was redefined by Kano and Kase (2000a, b) as small neritiform gastropods with (i) spiral ridges on the protoconch, (ii) the inclination of the protoconch against the teleoconch, and (iii) perpendicular, not inclined, prisms in the outer shell layer. The shell of *Pisulina* species consists of four layers: an outer layer of simple irregular prisms, middle layer of simple CL structure, myostracum, and inner layer of CCL structure with prismatic sublayers (Kano and Kase, 2000b; figs. 6, 7).

(6) Neritidae: All neritid taxa so far investigated share a four-layered shell consisting of an outer layer of calcitic prismatic structure, middle layer of aragonitic CL structure, myostracum, and inner layer of aragonitic CCL structure (Table 1). Their shells can be further classified into two types based on relative thickness of shell layers: marine species have a thicker outer layer with a thinner periostracum, while nonmarine species have a reduced outer layer with a well developed periostracum (Suzuki *et al.*, 1991). This difference is, however, considered to be induced by environmental factors, because thin shells protected by a thick periostracum occur in various distantly related brackish and freshwater mollusks.

(7) Phenacolepadidae: The only description for this family was given for *Cinnalepeta pulchella* in this study, and the difference from other families lies in the homogeneous structure of the outer layer.

Operculum of Recent Neritopsina

Neritopsine operculum exhibits a great diversification in the number of calcified layers, the coverage of the organic layer, the position of calcareous layer(s) on one or both sides of the organic layer, the presence or absence of apophysis, and the morphology of muscle scars.

(1) Neritopsidae: The exterior surface of the operculum of *Neritopsis radula* is covered with a thick callus without a nucleus and spiral lines; the interior is divided into a smooth semilunar zone at the abaxial side and a large projection with a radial striation at the adaxial side (Thiele, 1929: fig. 55; Wenz, 1938: fig. 1001; Knight *et al.*, 1960: fig. 182; Ponder, 1998: fig. 15.71C, D). This projection may be the hypertrophied homologue of the apophysis of other neritopsines, with its origin shifted toward the center. The absence of a spiral line on both surfaces and a large projection from the interior center is quite unique among Gastropoda. However, no microstructural data for this family have been published to date.

(2) Hydrocenidae: The operculum of *Georissa japonica* is calcified with an apophysis and three-layered: the organic
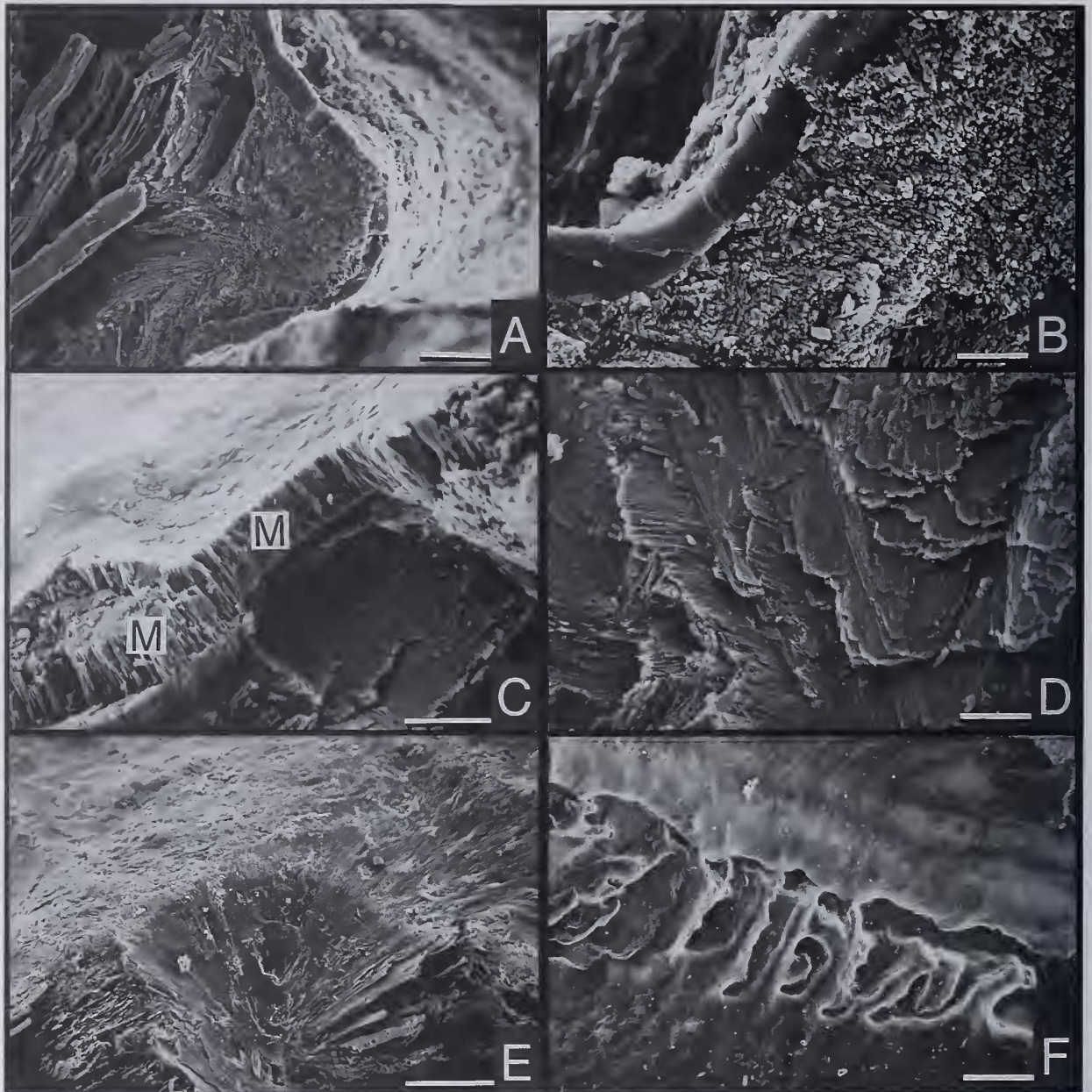
Figure 7. SEM micrographs of shell microstructure of *Cinnalepeta pulchella* (UMUT RM27952). **A.** Vertical fracture of the outer layer. Scale = 20 μm. **B.** Enlarged view of homogeneous structure. Scale = 5 μm. **C.** Vertical fracture of pedal muscle scar showing the myostracum overlying the middle layer. M = myostracum. Scale = 10 μm. **D.** Vertical fracture of CCL structure near the center of the shell. Scale = 10 μm. **E.** Oblique fracture (below) and outcrop surface (above) of CCL structure. Scale = 50 μm. **F.** Oblique view of pedal muscle scar near inner lip, showing irregular rough surface. Scale = 200 μm.

layer on the outermost surface is underlain by two aragonitic layers of irregular prismatic structure (Suzuki, *et al.*, 1991: fig. 5).

(3) Helicinidae: This family is highly specialized for Neritopsina in that Ceresinae and Proserpininae completely lack an operculum, while Helinicinae have a calcified operculum without an apophysis (Thompson, 1980). The

operculum of *Waldemaria japonica* has a single layer of calcitic blocky structure on an organic layer (Suzuki, *et al.*, 1991). Helicinids are strikingly different form other neritopsines in that calcification occurs only on the exterior surface, not interior of the organic layer.

(4) Titiscanidae: This shell-less taxon also lacks an operculum and is completely sluglike (Bergh, 1890; Taki,

Table 1. Published data on shell microstructure of the Recent Neritopsina.   BL = blocky, CCL = complex crossed lamellar, CL = simple crossed lamellar, HO = homogeneous, IPR = irregular prismatic, PCL = protocrossed lamellar, PR = prismatic.

Family	Genus	Shell microstructure		Inner layer	Reference
		Outer layer(s)		Inner layer	Reference
Neritopsidae	*Neritopsis*	CL		CL	Batten (1979)
	Neritopsis	CL		PCL, IPR, HO, CCL	Suzuki *et al.* (1991)
Hydrocenidae	*Georissa*	CL		PCL, IPR	Suzuki *et al.* (1991)
Helicinidae	*Waldemaria*	CL		PCL, IPR	Suzuki *et al.* (1991)
Neritiliidae	*Pisulina*	PR	CL	CCL	Kano and Kase (2000b)
Neritidae	*Nerita*	PR	CL	CCL	Bøggild (1930); Gainey and Wise (1980);This study
	Nerita	BL	CL	PCL	Suzuki *et al.* (1991)
	Neritina	PR	CL	CCL	Bøggild (1930)
	Neritina	BL	CL	PCL	Suzuki *et al.* (1991)
	Clithon	BL	CL	PCL	Suzuki *et al.* (1991)
	Neripteron	BL	CL	PCL	Suzuki *et al.* (1991)
	Septaria	BL	CL	PCL	Suzuki *et al.* (1991)
Phenacolepadidae	*Cinnalepeta*	HO	CL	CCL	This study

1955).

(5) Neritiliidae: In the species of *Pisulina,* the operculum is secreted with exterior corneous and interior calcareous layers (Kano and Kase, 2000b: figs. 8, 9, 11).   The small initial part containing the nucleus on the corneous layer is demarcated from the remaining part.   The muscle scars are divided into three areas: two elongate zones along the adaxial and basal margins, and a central one extending between the nuclear zone and apophysis.   The inner calcareous layers are formed of spherulitic prisms (Kano and Kase, 2000b: fig. 6F).

(6) Neritidae: The gross morphology of the neritid operculum is classified into two distinct types (see e.g. Starmühlner, 1993; Komatsu, 1986): (i) The operculum of *Septaria* (subfamily Septariinae) is embedded in the dorsal part of the foot.   The anterior left corner has a sharp projection which is supposedly homologous to the apophysis of other neritopsines on the left side.   (ii) The rest of the neritids (subfamilies Neritinae and Smaragdiinae) have a semilunar external operculum with a prominent apophysis.

The opercular microstructure of neritids is known to be variable, depending on habitats.   The marine neritids have a common opercular plan with a single exterior aragonitic prismatic layer, an organic layer, and two interior aragonitic prismatic layers (Suzuki *et al.*, 1991: fig. 5; this study: Figs. 4, 5).   The opercula of nonmarine species (*Neritina* and *Clithon*) have only two aragonitic prismatic layers covered by a well developed organic layer (Suzuki *et al.*, 1991).

The operculum of *Bathynerita naticoidea* (tentatively treated as a neritid here) dwelling exclusively in deep-sea hydrocarbon seeps is "partly calcified with a thicker calcareous layer where it is attached to the foot" (Warén and Bouchet, 1993), and the apophysis is absent.   Its operculum with only partial calcification is greatly different from those of shallow-water neritids.

(7) Phenacolepadidae: The opercular morphology of phenacolepadids can be divided into three distinct states. (i) The presence of a vestigial internal operculum with inte-

rior calcification and rudimentary apophysis was documented by Fretter (1984) in *Phenacolepas omanensis* and observed with SEM for the first time by Kimura and Kimura (1999: fig. 7C, D) in *Phenacolepas* sp.   (ii) The opercula of so-called "Shinkailepedidae" has double structure of calcified anterior and noncalcified posterior parts as described in *Shinkailepas* by Okutani *et al.* (1989: fig. 12) and Beck (1992: pl. 1, fig. 4) and in *Olgasolaris* by Beck (1992: pl. 5, fig. 4).   Double-layered nail-shaped operculum is strikingly convergent with that of the neritid genus *Septaria*.   (iii) The operculum is absent in *Cinnalepeta*, as described above.

Implication of neritopsine hard-part microstructures
It has been generally accepted that microstructural characters of the shells are useful for the understanding of molluscan higher taxonomy.   It is, however, necessary to check the correlation between taxonomic distribution of structural morphotype and phylogenetic relationships in the Recent taxa before comparing extant and extinct forms directly.

(1) Shell structure: As reviewed above, the patterns of shell structure of the Recent Neritopsina can be categorized into two major types: (i) Genera of three families, Neritidae, Phenacolepadidae, and Neritiliidae, all have four-layered shells in which inner CCL and middle CL layers are overlaid by a prismatic (in Neritidae and Neritiliidae) or homogeneous (in Phenacolepadidae) shell layer.   (ii) By contrast, other families such as Neritopsidae, Helicinidae, and Hydrocenidae secrete three-layered shells which consist mostly of CL/CCL structures and lack an additional outer layer.   This apparent difference between the two groups may be viewed as expressing the distinctness of their relationship, but it is still premature to present phylogenetic implication because of the lack of a reliable phylogenetic hypothesis.   The phylogenetic analysis has been conducted only in a part of Neritopsina by Holthuis (1995) and Sasaki (1998), and the phylogenetic status of Neritopsidae, Helicinidae, and Hydrocenidae is totally unknown.   The scarceness of struc-

tural data relative to the number of existing genera is also problematic so far as testing the stability of character states within each family.

Another unresolved problem is whether all of the taxa with a four-layered shell share a calcitic outer layer or not. Suzuki *et al.* (1991) revealed that at least the shell of neritids is constructed from a calcitic outer layer and otherwise aragonitic layers in contract to the entirely aragonitic shell of other families. They argued that this bimineralic composition is attributable to adaptation to a shallow aquatic environment, probably as a means of reinforcing the mechanical strength of the shell. Thus, it should be tested as a next step whether non-neritid four-layered shells are also made of two crystal forms of calcium carbonate. Concerning the outermost shell layer, Taylor and Reid (1990) revealed the parallel homoplastic addition of a calcitic outer layer in some genera within littorinid gastropods. This means that the convergence in conchological characters should necessarily be considered also at the microstructural level in other groups of molluscs.

(2) Opercular structure: The opercular structure can be divided into several types as a result of the above comparison: (i) three (single exterior and two interior) aragonitic layers in marine neritids, (ii) two interior aragonitic layers in Hydrocenidae and nonmarine neritids, (iii) single calcitic exterior layer without interior calcification in Helicininae, (iv) interiorly calcified operculum with unknown layer distribution in Neritiliidae and a part of Phenacolepadidae, and (v) absence of an operculum in Titiscaniidae and in part in the Phenacolepadidae and Helicinidae. Thus, a single similar state often occurs across several different families, and also several different states can coexist within the same family. At the family level the similarity and dissimilarity in opercular structure are very difficult to explain in the phylogenetic context.

In connection with nonphylogenetic factors, the less calcified opercula in nonmarine neritids as compare with marine confamilial members may be explained as a consequence of adaptation to low-salinity environments (Suzuki *et al.*, 1991). However, in other taxa, there is no clear correlation between opercular structure and habitat selection. The marked differences in neritopsine opercular structure is difficult to understand also in terms of adaptation. The possession of apophysis is presumably under phylogenetic control within Neritopsina, and at the same time, it is a convergent state also found in caenogastropod rissoideans. The peglike structure has possibly arisen to increase the area of muscular attachment in this case.

Because of the insufficient resolution of neritopsine phylogeny and the lack of mineralogical data in part, the evolutionary scenario of neritopsine hard parts remains largely speculative at present. For further studies, exoskeletal structure including mineralogical characters should be investigated more comprehensively in whole extant and extinct neritopsines together with the comparative anatomy and molecular phylogeny of the Recent species.

Acknowledgments

Reference

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